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CHROMOSOME STUDIES ON THE DIPTERA

III. ADDITIONAL TYPES OF CHROMOSOME GROUPS IN THE DROSOPHILIDÆ

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IN connection with other work on the Drosophilas I have for some time been engaged in a comparative study of their chromosomes, with especial reference to possible phylogenetic relationships between different species. A short preliminary report of this study was published two years ago (Metz, '14) after five types of chromosome groups had been found among eleven species. More recently I have studied fifteen additional species of *Drosophila,* one of *Cladochæta* and two of *Scaptomyza* (related genera), and have found several more types of chromosome groups. Altogether twelve main types and several sub-types have been identified—a series more extensive, I believe, than any heretofore recorded among allied species. Of these twelve types all but one are represented in the genus *Drosophila.*

The study has not yet advanced far enough to fulfil the purpose for which it was originally undertaken, but in view of the widespread interest recently attracted to the Drosophilas as objects of genetic research it seems desirable briefly to describe the chromosomes of the species thus far examined without awaiting the completion of the original investigation. In doing this I shall endeavor merely to give an accurate presentation of the chromosomal data, without dwelling on the theoretical considerations they may suggest, considerations which can receive adequate treatment only after many more species have been examined.

Since in almost every case larval or pupal stages are the only ones suitable for study, it has been necessary to breed the various species in confinement in order to determine their chromosome groups. As a result only about half of those collected have been studied cytologically. Other determinations will be reported in the future as they are obtained.

The material has been secured from four regions, New York, Massachusetts, Alabama and Cuba, with the exception of one species (not found in these localities) from California and Oregon.[1] Fourteen of the twenty-nine species are undescribed and are here given the manuscript names of Dr. A. H. Sturtevant.[2] Descriptions of them are in press.

Most of the chromosome descriptions in the present paper are taken from pedigree material, either first or second generation from wild flies, and the results have been checked up in such a way as to make it very improbable that serious errors have crept in. As mentioned in previous papers the chromosomes of these flies stand out with diagrammatic clearness when favorable figures are secured; and since they are uniformly arranged in pairs and are often of various sizes they offer admirable material for a comparative study. This makes it possible to classify the members of each chromosome group according to their size and shape, and to assort the groups into definite types according to their configuration.

DESCRIPTION OF TYPES

The terminology used in describing the chromosomes will be the same as that used in my previous paper ('14).

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[1] The collections, of course, include only a fraction of the existing species within these areas, to say nothing of those in surrounding regions. For more detailed locality references see description of types.

[2] This investigation would have been practically impossible without the cooperation of many friends. In addition to Dr. Sturtevant, to whom I owe all of the identifications, and cultures of several species, I am under obligation to Professor F. S. Earle, Dr. Carlos de la Torre and Mr. C. T. Ramsden for many courtesies shown to me while collecting in Cuba, and to Messrs, L. L. Gardner and G. F. Sykes for Pacific coast material, including *D. obscura*.

Certain recurring kinds will be distinguished in advance and will be designated by name or letter in the specific descriptions. These are as follows:

V. Long, V-, U-, or dumb-bell shaped chromosomes, attached to the spindle at the median constricted portion (apex of the *V*).

r. Rod-like, straight chromosomes, approximately half the length of *V*, attached to the spindle at one end, and radially arranged in metaphase.

c. Short, curved chromosomes, differing from *r* only in form and (probably) in having a median attachment to the spindle.

m.[3] Minute, spherical or slightly elongate chromosomes, usually located in the center of the metaphase plate.

To these symbols must be added *XX* and *XY*, used to designate the sex chromosomes wherever they have been definitely identified. In some species they are straight, in others V-shaped. Identification of the sex chromosomes and determination of the *XY* relations in the males has been one of the most difficult features of the study, owing to the extreme scarcity of spermatogonial and spermatocyte figures; but it has been made in as many cases as possible and has been of great usefulness in comparing different groups.

The order or sequence in which the types are described is a purely arbitrary one, and is not intended to indicate any genetic relationship.

In order to avoid duplication of figures chromosome groups which have previously been described and figured are not reproduced here unless they are of especial interest. The series of types as a whole may best be understood from an examination of diagrams *A* to *L*, which represent schematically, but accurately, the twelve main types.

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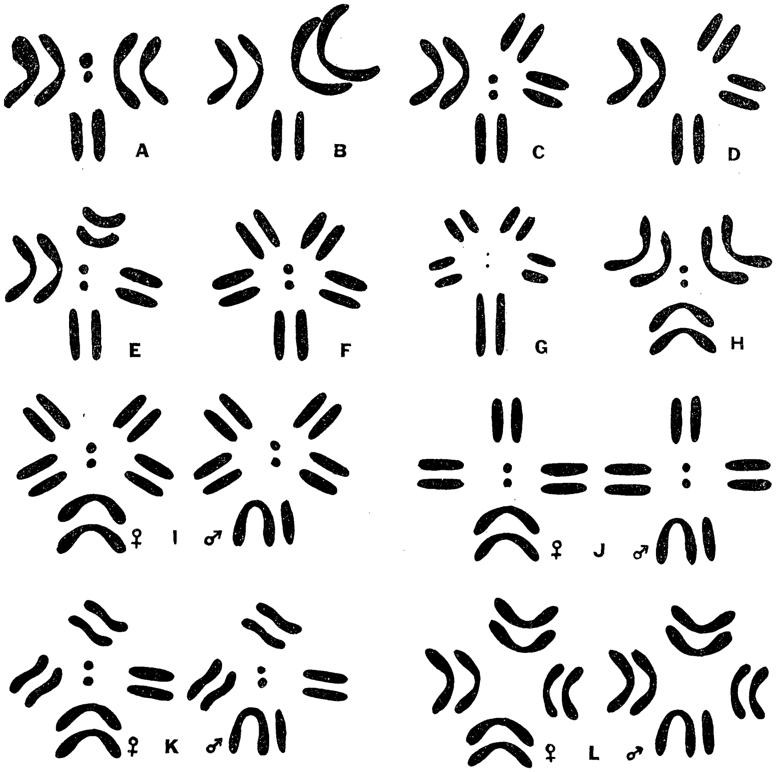
[3] The term *m*-chromosome, borrowed from Wilson ('05), is used here in a purely descriptive sense, and is not intended to signify any relationship with the *m*-chromosomes of the Hemiptera.



Type A

Represented by

Drosophila ampelophila Loew. Cosmopolitan.[4] (See Stevens, '08, Figs. 57–60, 80–82, Metz, '14, Figs. 4 and 5, Bridges, '16, Figs. 1–4, Metz, '16, Fig. 19.)

Drosophila amoena Loew. New York. (Metz, '14, Figs. 1–3, Metz, '16, Figs. 13–16.)

Drosophila busckii Coq. New York. (Metz, '16, Figs. 17 and 18.)

Drosophila bromeliae Sturtevant mss. Cuba. (Fig. 1.)

Drosophila dimidiata Loew. Alabama. (Metz, '16, Fig. 20.)

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[4] With the exception of this species, which has been studied by several investigators, localities cited are those in which my cytological material has been obtained.

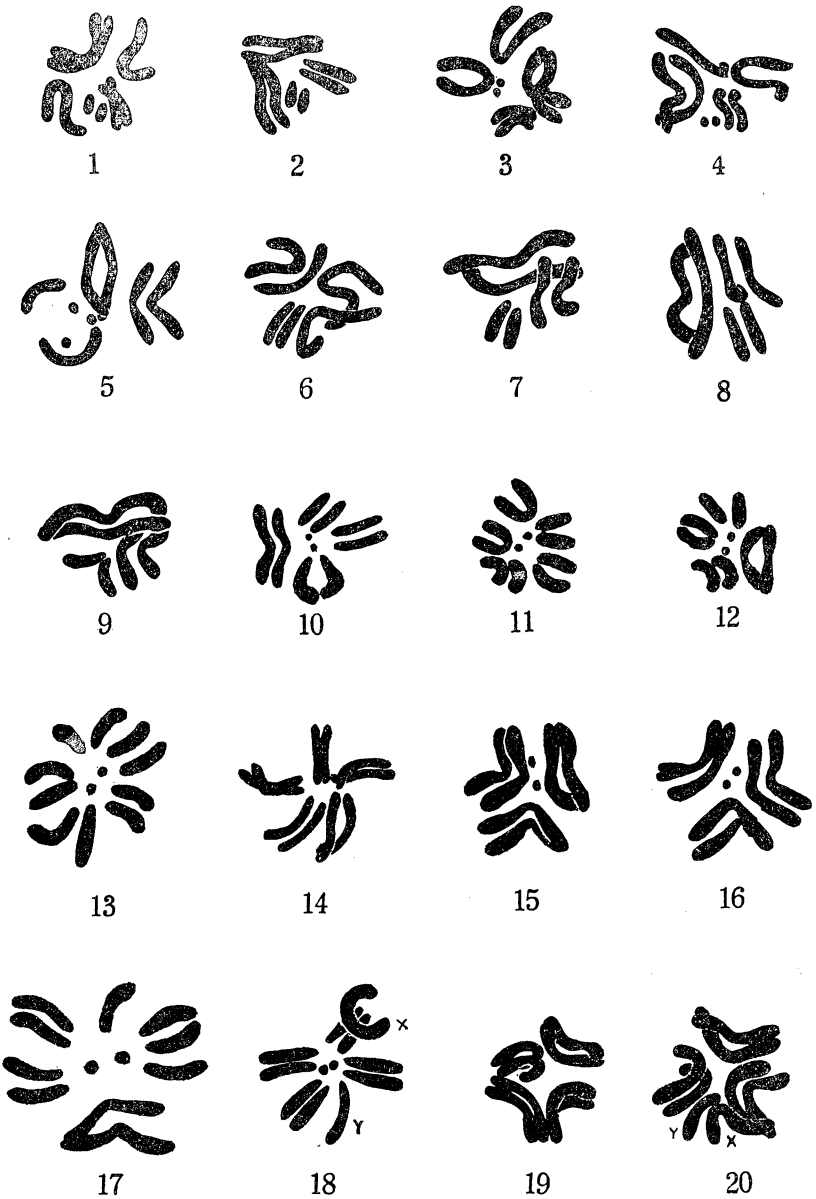

PLATE I

Explanation of Figures

All figures were drawn with the aid of a camera lucida, using Zeiss 1.5 mm. apochromatic objective and compensating ocular number 12, with tube length of 160 mm. The drawings are reproduced natural size. With the exception of number 17 all are taken from sections cut 5 microns thick.

Drosophila floræ Sturtevant mss. Cuba. (Fig. 2.)
Drosophila limbata Will. Cuba. (Metz, '16, Figs. 10–12.
Drosophila procnemis Will. Cuba. (Metz, '16, Figs. 34–36.)
Drosophila quinaria Loew. New York. (Metz, '14, Fig. 7.)
Drosophila robusta Sturtevant mss. New York. (Figs. 3 and 4; Metz, '16, Figs. 7–9.)
Drosophila saltans Sturtevant mss. Cuba.
Drosophila pallida Will. Cuba.
Scaptomyza graminum Fall. New York. (Fig. 5; Metz, '16, Figs. 4–6.)

This is type I of my previous paper, and is the prevailing type among the species studied, being represented by thirteen of the total twenty-nine. It consists of two pairs of long, V-shaped chromosomes, one pair of straight sex chromosomes, and one pair of *m*-chromosomes.

Slight modifications of this type are found in certain species, usually characterized by peculiarities in the sex chromosome pair. In *D. ampelophila* it appears from the work of Bridges ('16) that the *Y*-chromosome, instead of being straight as is the *X*-chromosome, is hook-shaped or V-shaped, although never large enough to be confused with the V-shaped euchromosomes. My observations confirm those of Bridges in this regard with the exception of two figures in which *X* and *Y* appear equal and straight. Perhaps these are due to accident, but they are entire figures and normal in other respects.

FIG. 1. *Drosophila bromeliæ* Sturtevant mss., spermatogonium.
FIG. 2. *Drosophila floræ* Stt. mss., ovarian cell.
FIGS. 3 and 4. *Drosophila robusta* Stt. mss., spermatogonia.
FIG. 5. *Scaptomyza graminum*, spermatogonium.
FIGS. 6–9. *Drosophila carlei* Stt. mss., ovarian cells.
FIG. 10. *Scaptomyza adusta*, ovarian cell.
FIGS. 11 and 12. *Drosophila neglecta* Stt. mss., ovarian cells.
FIG. 13. *Drosophila similis*, ovarian cell.
FIG. 14. *Drosophila cardini* Stt. mss., ovarian cell. The *m*-chromosomes are not visible in this figure, but are evident in other cells of the same ovary.
FIGS. 15 and 16. *Cladochæta nebulosa*, ovarian cells.
FIG. 17. *Drosophila repleta*, variety *b*, ovarian cell. Taken from an aceto-carmine smear preparation.
FIG. 18. Same, spermatogonium, from a section.
FIG. 19. *Drosophila caribea* Stt. mss., ovarian cell.
FIG. 20. Same, spermatogonium.

In *D. amoena* and *S. graminum* spermatogonial figures indicate that *X* and *Y* are unequal and straight (Fig. 5, and Metz, '14, Figs. 2 and 3); while in *D. busckii, D. floræ, D. bromeliæ, D. robusta* and *D. limbata* no inequality is evident. The other species have not been examined with respect to spermatogonial groups. In *D. robusta* the rod-like members (sex chromosomes?) appear to be hook-shaped and to be attached sub-terminally to the spindle in much the same manner as the *Y*-chromo some in *ampelophila*.

Another modification or sub-type is represented by *D. floræ* and *D. bromeliæ,* in which the *m*-chromosomes are materially larger than in the other species. Indeed, those of the former are so large as to suggest a transition between *m*-chromosomes and *r*-chromosomes.

Type B

Represented by

Drosophila earlei Sturtevant mss. Cuba. (Figs. 6–9.)

This interesting type consists of one short rod-like pair and two large V-shaped pairs, one of which is much longer than the other. No trace of *m*-chromosomes has thus far been found in the fifteen or twenty figures I have studied. Unfortunately I have not yet secured good spermatogonial figures and am unable to identify the sex chromosomes.

In many respects type *B* is of greater interest than any other type of chromosome group I have studied, for it not only contains the smallest number of chromosomes thus far found among the higher flies,[5] but each of its three pairs is conspicuously different from either of the other two, making possible an individual identification of the chromosomes not obtainable, with such a degree of certainty, in any other known species of *Diptera.* If a genetic continuity of chromosomes be admitted there can be no question that here each paternal chromosome associates with its corresponding maternal mate. (See Metz, '16, p. 251.)

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[5] Two species of Culicidæ (*Anopheles punctipennis* and *Culex pipiens*) also have three pairs of chromosomes. See Stevens, '11.

Type C

Represented by

Drosophila ornatipennis Will. Cuba. (Metz, '16, Fig. 21.)

Scaptomyza adusta Loew. New York. (Fig. 10; Metz, '16, Fig. 22.)

Type *C* corresponds to type IV of my previous paper ('14), but the single species formerly referred to it has been transferred to type *E*. Chromosome groups of type *C* are composed of one large V-shaped pair, one long, straight sex chromosome pair, two shorter rod-like pairs and one small *m*-pair. In both species spermatogonial figures show a noticeable inequality between *X* and *Y*; thus identifying the sex chromosomes.

Type D

Represented by

Drosophila tripunctata Loew. New York. (Metz, '14, Figs. 21–26.)

Type *D* corresponds to type *V* of my previous paper ('14) and includes only one species. It differs from type *C* in lacking the *m*-chromosome pair, and in sex chromosome relations. *X* and *Y* are apparently equal in size and similar to the rod-like euchromosomes. Their identification is based solely upon their precocious contraction in prophase (see Metz, '14, p. 52), and hence may be held with some reserve, but from analogy with species of types *A* and *C* it seems highly probable that the identification is correct.

Many preparations have been made from material of this species in an attempt to discover an *m*-chromosome pair such as is found in most other species of *Drosophila*, but although stocks have been obtained from several localities and various methods of fixation have been used no trace of the pair has been observed.

Type E

Represented by

- *Drosophila melanica* Sturtevant mss. (two varieties). New York, Alabama. (Figs. 11, 12; Metz, '16, Figs. 23–26.)

The chromosomes of this species resemble those of type *C,* with the exception of one of the short pairs, which is curved or U-shaped instead of straight. Such a difference in shape is apparently associated with a different mode of attachment to the spindle, and seems to be a characteristic feature. In my previous paper ('14) *D. melanica* was cited as an example of the type corresponding to *C* of the present paper, and the curved shape of this pair was not considered significant; but more recently I have examined many additional figures and have become convinced that the character is normal and sufficient to distinguish the two types. The few spermatogonial figures I have examined closely resemble those of female groups and give no evidence of an unequal *XY* pair.

The two varieties[6] of *D. melanica,* although refusing to hybridize, are very similar in external appearance and indistinguishable in chromosomal characters.

Type F

Represented by

- *Drosophila virilis* Sturtevant mss. New York City. (Metz, '14, Figs. 11–13, Metz, '16, Fig. 2.)
- *Drosophila similis* Will. Cuba. (Fig. 13.)
- *Drosophila ramsdeni* Sturtevant mss. Cuba. (Metz, '14, Fig. 10, Metz, '16, Fig. 3.)
- *Drosophila cardini* Sturtevant mss. Cuba. (Fig. 14.)
- *Drosophila modesta* Sturtevant mss. Alabama.
- *Drosophila repleta* Woll., variety *a.*[7] Cuba, Texas. (Metz, '14, Figs. 8 and 9.)

This type (Type II of the previous paper) differs from *C* in having two pairs of rod-like chromosomes in place of the large V-shaped pair, and from type *A* in possessing four rod-like pairs in place of two V-pairs. Next to type *A* this type is of most frequent occurrence, being represented by six of the twenty-nine species.

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[6] For discussion of these see forthcoming paper by Dr. A. H. Sturtevant.

[7] See also type *I.*

Spermatogonial figures have been examined in only one of these species, *D. virilis*, and here no conspicuous inequality between *X* and *Y* is to be seen. One pair of chromosomes appears to be larger in nearly all figures of either sex, and a slight difference in length between the two members of this pair may be seen in some male figures, but it may be purely accidental.

Type G

Represented by

Drosophila funebris Fabr. New York, California, North Dakota. (Metz, '14, Figs. 14–17,[8] Metz, '16, Figs. 27–33.)

This interesting type (type III of the previous paper) is apparently a modification of type *F*, but differs from it in the relative proportions of all of the chromosomes. The *m*-chromosomes are so minute in most specimens as scarcely to be visible, and for this reason were entirely overlooked at first. Their conspicuousness doubtless varies with the amount and kind of stain, and with the fixative used, but even after making full allowance for this there can be no doubt that the pair is much smaller here than in most other species. Otherwise the type is characterized by the smaller size of the short, rod-like chromosomes and the greater length of the longest (sex chromosome?) pair. As in the preceding case no conspicuously unequal *XY* pair is to be found in the males, although a noticeable difference between the two large chromosomes may be seen in some of the figures.

Type H

Represented by

Cladochaeta nebulosa Coq. Cuba. (Figs. 15 and 16.)

This species—the only known member of the genus—is included in the present review because of its obvious relationship to the true Drosophilas. The type of chromosome group which it represents is the only one of the twelve not thus far found in some species of *Drosophila,* and its general similarity to some of the *Drosophila* types is marked. Female groups consist of three similar pairs of long, V-shaped chromosomes and one small pair of *m*-chromosomes. Unfortunately the species breeds very poorly in confinement and no male preparations were secured. It is almost certain, however, that one of the long pairs is the sex chromosome pair.

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[8] Fig. 14 (Metz, '14) and Fig. 27 (Metz, '16) are from the same cell; the latter drawn after the *m*-chromosomes were discovered.

Type I

Represented by

Drosophila repleta Woll., variety *b*. New York, Massachusetts, California. (Figs. 17 and 18; Metz, '16, Figs. 39–41.)

In my 1914 paper *D. repleta* was referred to the type corresponding to *F* of the present study, but it is now evident that two very similar but distinct varieties of the species occur, characterized, among other things, by decidedly different sex chromosomes. In one, the sex chromosomes are short and rod-like in the female and presumably so in the male, while in the other they are long and V-shaped in the female and markedly unequal in the male. The latter represents the present type *I*. The difference between the two may be readily appreciated by an examination of diagrams *F* and *I*. Although it relates only to the sex chromosomes it is very striking in the females, and easily separates the two varieties into distinct types. The fact that the two forms can not be induced to hybridize lends support to the chromosomal evidence of their distinctness, but externally they are astonishingly similar and are referred to the same species by Sturtevant.[9]

[9] It may be noted that these are not the "light and dark" varieties described by Sturtevant ('15), both of which belong to type I.

Type J

Represented by

Drosophila obscura Fall. California and Oregon. (Metz, '16, Figs. 44–50.)

Ovarian cells of *D. obscura* contain three rod-like euchromosome pairs, one small *m*-chromosome pair and one very long, V-shaped sex chromosome pair (diagram *J*, ♀). In the male the sex chromosomes are very dissimilar, *Y* being straight and only about half as long as *X*.

Type K

Represented by

Drosophila affinis Sturtevant mss. Alabama. (Metz, '16, Figs. 42 and 43.)

In general this type resembles the last, but differs in having two S-, or hook-shaped pairs in place of rod-like ones. Apparently this peculiar shape is due to a subterminal attachment to the spindle, although I have been unable to get figures actually demonstrating the attachment. In some cases one or both pairs extend radially from the center of the figure as if they were attached terminally, but usually their position is characteristically that described above. In any event the two pairs are readily distinguished from any others of the group, unlike those of *D. obscura*.

Type L

Represented by

Drosophila caribea Sturtevant mss. Cuba, Panama. (Figs. 19 and 20.)

This type is radically different from any of those described above, and like the two preceding is represented by only one species. Female (ovarian) groups are composed of four long V-shaped pairs of chromosomes, one, of which is shorter than the other three. In the male one pair is conspicuously unequal, much as in types *I*, *J* and *K*, but I have been unable to determine with certainty whether this is the small pair or one of the large ones. It is represented as a large one in the diagram (*L*, ♂).

Several of the species contained in this survey have been, or are being used in genetical studies. With the exception of the well-known *D. ampelophila* these are included in the following list, together with references to literature dealing with them, so far as known to me:

D. repleta, type *H.,* Sturtevant, '15, Hyde, '15.
D. affinis, type *J.* Hyde, '15.
D. tripunctata, type *D.* Metz and Metz, '15.
D. virilis, type *F.* Metz and Metz, '15.
D. similis, type *F.* In press.
D. obscura, type *I.* In press.

LITERATURE CITED

Bridges, C. B. 1916. Non-disjunction as Proof of the Chromosome Theory of Heredity. Genetics, I, p. 1.

Hyde, R. R. 1915. The Origin of a New Eye Color in *Drosophila repleta,* and Its Behavior in Heredity. AMER. NAT., 49, p. 183.

1915. A Wing Mutation in a New Species of *Drosophila.* Ibid., p. 185.

Metz, C. W. 1914. Chromosome Studies in the Diptera I. A Preliminary Survey of Five Different Types of Chromosome Groups in the Genus *Drosophila.* *Jour. Exp. Zool.,* 17, p. 45.

Metz and Metz. 1915. Mutations in Two Species of *Drosophila.* AMER. NAT., 49, p. 187.

Metz, C. W. 1916. Chromosome Studies in the Diptera. II. The Paired Association of Chromosomes in the Diptera and Its Significance. *Jour. Exp. Zool.,* 21, p. 213.

Stevens, N. M. 1908. A Study of the Germ Cells of Certain Diptera, . . . *Jour. Exp. Zool.,* 5, p. 359.

Stevens, N. M. 1911. Further Studies on Heterochromosomes in Mosquitoes. *Biol. Bull.,* 20, p. 109.

Sturtevant, A. H. 1915. A Sex-linked Character in *Drosophila repleta.* AMER. NAT., 49, p. 190.

Wilson E. B. 1905. Studies on Chromosomes. II. *Jour. Exp. Zool.,* 2, p. 508.